Parasitism (Hymenoptera: Braconidae, Microgastrinae) in an apparently adventitious colony of Lymantria dispar (Linnaeus) (Lepidoptera: Lymantriidae) in southern England, with speculations on the biology of Glyptapanteles porthetriae (Muesebeck)

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Synopsis

A small, highly localised and apparently adventitious colony of the lymantriid moth *Lymantria dispar* was discovered in southern England and found to be parasitised by two species of solitary microgastrine Braconidae (Hymenoptera), viz. *Cotesia melanoscelus* and *Glyptapanteles porthetriae*. While the former is a common and plurivoltine British resident with other lymantriid hosts, the latter is believed to be dependent on *L. dispar* and has not previously been found in Britain. Partly to account for its presence, but also to explain aspects of the confusing literature on this species, it is speculated that *G. porthetriae* may be predominantly univoltine and may oviposit in late summer into the embryonic *L. dispar* larvae that are known to overwinter fully developed in their eggs. Its presence in southern England might then have resulted from the importation of a parasitised *L. dispar* egg batch.

Key words: British Isles, Lymantriidae, Lymantria dispar, life cycle, voltinism, parasitoids, Braconidae, Microgastrinae, Pteromalidae, Glyptapanteles porthetriae, Cotesia melanoscelus, Pteromalus chrysos.

On 18.v.2007 one of us (MJS) noticed several small and unfamiliar caterpillars feeding on a group of stunted *Quercus robur* L. growing at the edge of a salt marsh at Hengistbury Head LNR, Bournemouth (V.C. 11). Two days later some had moulted and were then readily identified as *Lymantria dispar* (Linnaeus). A few were also found feeding on adjacent *Betula pendula* Roth and *Quercus ilex* L.

Several of the smaller larvae, in their second and third instars and fully exposed on the upper surfaces of leaves, were straddling solitary, white parasitoid cocoons (*ca* 4 mm long), aligned with and positioned under the posterior half of their bodies. For several days after parasitoid cocoon formation, these moribund host larvae remained alive and, when disturbed, were capable of making strong, sideways thrashing movements of their anterior half, but were otherwise quiescent. It was estimated that at least half of the early to middle instar *L. dispar* larvae succumbed to parasitism, out of a

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population estimated to be 200–300. Several collections of host-plus-cocoon pairs were made by MJS on 20.v.2007, 8.vi.2007 and 22.vi. 2007 and sent to MRS for identification of the parasitoids. By the end of June all healthy caterpillars of this univoltine moth had completed their feeding, while the moribund parasitised hosts had mostly wasted and disappeared or, at least, the associated parasitoids had either emerged successfully or themselves had been parasitised in their cocoons by the pteromalid *Pteromalus chrysos* (Walker) (det. R. R. Askew). This is a common chalcidoid that attacks small cocoons such as those of Microgastrinae, when its relationship with respect to a lepidopterous host is that of pseudohyperparasitoid; it was reared from some cocoons of both species of primary parasitoid recorded below.

Two species of primary parasitoids emerged from the cocoons, both microgastrine Braconidae formerly included in the traditional genus Apanteles Foerster (cf. Nixon, 1973; 1974), but reclassified by Mason (1981) into the genera Cotesia Cameron and Glyptapanteles Ashmead respectively. From just off-white (cream) cocoons, 1° , 1° , 1° Cotesia melanoscelus (Ratzeburg) (= solitarius (Ratzeburg)) emerged during June. This is a well known solitary parasitoid of several species of Lymantriidae which has been transported from Europe to be used in classical biological control programmes against both L. dispar (Crossman, 1922) and Leucoma salicis (Linnaeus) (Parker, 1935) in North America, where it has become established (Dowden, 1962; Marsh, 1979). It is a usually common parasitoid in populations of L. salicis in Britain and it also attacks Orgvia antiqua (Linnaeus) regularly. Cotesia melanoscelus is always solitary, but it is one of several plurivoltine Cotesia species that habitually undergoes several generations on a single host generation and is able to develop in host larvae of a wide range of sizes. Further, it can overwinter within an overwintering host caterpillar, or as a prepupa in its own cocoon. It is not at all surprising that C. melanoscelus was locally on hand to discover and attack the presumably adventitious L. dispar population, as at least one of its regular hosts (O. antiqua) is established at the site.

The majority of the cocoons received by MRS were more starkly white and fractionally larger and more elongate. From these, $6 \ ^{\circ}$, $1 \ ^{\circ}$ *Glyptapanteles porthetriae* (Muesebeck) emerged between the end of May and the end of June 2007. This species has not previously been recorded in Britain. However, it has been reported to be the commonest parasitoid of *L. dispar* larvae in some parts of Europe (Burgess & Crossman, 1929; Reardon, Statler & McLane, 1973; Fuester *et al.*, 1988). Following an early history of misidentification (cf. Burgess & Crossman, 1929; Marsh, 1979), it was described as a new species (Muesebeck, 1928) during the screening of European populations of *L. dispar* for possible classical biological control agents to be used against the latter in North America.

However, despite numerous attempts to introduce it, *G. porthetriae* has not become established in North America (Dowden, 1962; Marsh, 1979) and, indeed, it was only brought into culture there successfully following the establishment of a continuously-brooded laboratory strain of its *L. dispar* host (Reardon, Statler & McLane, 1973) and hence a continuous supply of early instar host larvae. (Previously it had been cultured for one to two generations

through young larvae hatching from egg batches retarded by chilling; cf. Burgess & Crossman, 1929.) All investigations have shown that G. porthetriae is a strictly solitary parasitoid – Nixon's (1973) statement that it is gregarious, in the key-work most widely used for the identification of European *Glyptapanteles* species, is an unfortunate error. In the laboratory it attacks only the earliest instar larvae of the host with good (though far from perfect) success (Nussbaumer & Schopf, 2000). This restriction to early instar hosts led to the widespread supposition that the failure of G, porthetriae to become established in North America was the result of its presumed (but completely unknown!) late summer hosts in Europe, by means of which it supposedly completed its annual life cycle, not being matched in North America (cf. Burgess & Crossman, 1929; Reardon, Statler & McLane, 1973; Marsh, 1979; Fuester et al., 1988; but see also Raffa, 1977). This presumption of alternating hosts, as well as its early history of misidentification, has resulted in some confusing, ambiguous and inconsistent statements in the literature on G. porthetriae.

It is astonishing that, despite considerable effort to elucidate it, the allimportant means of completing its annual life cycle remains unknown for such a major – even dominant – parasitoid in native populations of such an economically important species of Lepidoptera. However, we believe there are strong clues. The adult female parasitoid has, even for a *Glyptapanteles* species, an unusually pronounced keel-like hypopygium (= the last metasomal sternite, supporting the ovipositor) that is much more developed than would seem to be adaptive for ovipositing into exposed early instar larvae of *L. dispar*, and this morphological feature suggests a more concealed host. The overwintering strategy of *L. dispar*, a univoltine moth whose eggs are laid in large batches in the middle of summer and are deeply covered in hair scales from the female's abdomen, may provide another clue. These eggs develop quickly to the fullyformed first instar larval stage, but then do not hatch until the following spring (cf. McManus *et al.*, 1992).

As far as we can tell from the existing literature, there has been no consideration (or test) of the hypothesis given here, viz. that G. porthetriae is (locally) monophagous and normally (or largely) univoltine, habitually using its attenuated metasoma to probe the hair-covered egg masses of the host in the middle of summer and oviposit into what are essentially first instar L. dispar larvae inside their eggs; then overwintering (probably as a first instar larva) within these diapausing hosts until resuming development once the host larvae hatch and start feeding in the spring. A parasitoid behaving in such a way would not necessarily be expected to reject early instar hosts that had become free-ranging larvae (indeed, in some Microgastrinae known to attack pre-hatched larvae in this way there is facultative plasticity: cf. Shaw & Huddleston, 1991), so this hypothesis is not at variance with the success in bringing the parasitoid into culture when a continuous supply of first instar L. dispar larvae is available for oviposition (Reardon, Statler & McLane, 1973). However, the hypothesis does require G. porthetriae adults to be capable of existing in summer for a small number of weeks. This does not seem so very improbable, especially in view of the positive results during shipment (literally) of adults from Europe to North America recorded by Burgess & Crossman (1929).

Our hypothesis might very easily explain why the hypopygium is so much more extended in G. porthetriae than in the congeneric G. liparidis (Bouché), which also parasitises L. dispar (Nixon, 1973; Marsh, 1979). If pre-feeding hosts are the favoured stage for attack, it might also explain why only 68% of hosts apparently parasitised at the end of their first instar went on to produce parasitoids in the laboratory experiments undertaken by Nussbaumer & Schopf (2000), while levels of parasitism in some European field populations would seem to suggest a very much higher success rate (cf. Burgess & Crossman, 1929). In the context of our own observations, it could explain how the parasitoid came to be present in an isolated British population of the nonnative L. dispar so small and localised that it seems probable that it first arose that year and resulted from a single egg batch, conceivably imported (i.e. we suggest the egg batch may have already been parasitised soon after being laid in a part of Europe where both host and parasitoid were established). Although at first sight our hypothesis seems not so readily to explain the failure of G. porthetriae to become established in North America, confusion over its life history might well have resulted in most or possibly all releases being made at essentially unfavourable times of year (this could presumably be checked from unpublished USDA records).

In any case, it is to be hoped that somebody with the opportunity to do so will be motivated to test the hypothesis that *G. porthetriae* is a largely univoltine specialist parasitoid of *L. dispar* that preferentially oviposits into developed host eggs and does not depend on alternate hosts. If this proves to be the case, such an understanding of the life cycle of *G. porthetriae* – an extremely important parasitoid of *L. dispar* in Europe – may at last be the key to its successful manipulation as a biological control agent in North America.

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